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Potential impacts of ocean acidification on the Puget Sound food web

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Ecosystem impacts of ocean acidification (OA) were explored by imposing scenarios designed to mimic OA on a food web model of Puget Sound, a large estuary in northwestern USA. The productivity of functional groups containing mostly calcifiers was decreased while still allowing other species groups to respond to the scenarios in a dynamic way through indirect effects. Results focus on changes in ecosystem services and structure. Sometimes the direct and indirect effects of OA countered each other due to interactions between predators and prey within the food web, leading to little change in the food web. In other cases, direct and indirect effects caused greater change in the food web than anticipated from direct effects alone. Results were strongly affected by the group on which OA was directly imposed, with changes in copepod productivity being the most influential. While there is much uncertainty in our predictions, focusing on the complex interactions among species, and between species and their environment, will yield better understanding of how ecosystems may respond to OA.

Keywords: copepods, Ecopath with Ecosim, ecosystem services, fisheries management, food webs, ocean acidification, trophic cascades.

Introduction

Global oceans have absorbed about a quarter of the carbon dioxide released by human activities since the Industrial Revolution, leading to an ~30% increase in the concentration of H^+ and a drop in pH of ~0.1 units (Caldeira and Wickett, 2003; Feely et al., 2004; Hauri et al., 2009). If atmospheric carbon dioxide concentrations rise as expected, the average surface ocean pH will likely drop 0.3–0.4 units by the end of this century, possibly reaching its lowest value in over 40 million years (Caldeira and Wickett, 2003; Pelejero et al., 2010). This human-induced change, termed ocean acidification (OA), may occur ~100 times faster than the changes in ocean pH during Earth's recent glacial-interglacial transitions (Pelejero et al., 2010). Compounding the effects of carbon dioxide, coastal waters are also acidified by nutrient run-off and sulphur and nitrogen emissions (Doney et al., 2007; Feely et al., 2010).

The state of knowledge on the impacts of OA on marine organisms is in its infancy, yet it is clear that OA can cause a variety of responses (Kroeker et al., 2010). In particular, species with calcium carbonate structures may be negatively impacted by OA, though species' sensitivity will vary with taxonomy and other factors (Kroeker et al., 2010). The physiological challenges associated with building and maintaining calcium carbonate structures in low-pH environments are most likely mediated through energy demands and allocation (Cohen and Holcomb, 2009). The fossil record from several marine ecosystems indicates that past acidification events were contemporaneous with mass extinctions, suggesting that OA may overwhelm evolutionary processes and reorganize ecosystems (Hautmann et al., 2008; Kump et al., 2009; Pelejero et al., 2010). Observations from natural CO_2 vents show that increases in CO_2 can substantially alter marine communities (Hall-Spencer et al., 2008; Kroeker et al., 2011; Fabricius et al., 2011). It is imperative that marine resource managers understand the potential effects of OA on ecosystems already perturbed by numerous internal and external drivers.

Puget Sound is a fjordal estuary located in northwestern continental USA, with an oceanography that naturally leads to the development and maintenance of low-pH waters. Marine waters entering from the adjacent California Current large marine ecosystem have low pH because they typically come from depth via either the Juan de Fuca Trench or upwelling processes (Feely et al., 2008). Shallow sills in the Puget Sound bathymetry force deep, low-pH

waters to the surface, while tributaries draining the surrounding lowlands and mountain ranges deposit low-pH, low alkalinity waters, further decreasing Puget Sound's pH and buffering capacity. Biological activity and restrictions in water flow contribute to high pH variability observed in this and other estuaries (Hinga, 2002; Hofmann et al., 2011). Subsurface waters in Puget Sound's main basin are undersaturated with respect to aragonite in both the winter and summer (Feely et al., 2010). Thus, OA is imposed on complex pH patterns that exist in Puget Sound naturally, and has already caused a decrease in pH of 0.05−0.15 units and in surface aragonite saturation state of 0.09−0.33 (Feely et al., 2010).

Research on the biological impacts of OA has focused mainly on direct species-level effects. Scaling predictions of the general impacts of OA to full ecosystems, such as Puget Sound, requires knowledge of the extent to which species are affected by OA and the manner in which they interact with other species, including those not directly impacted by OA. We explored the potential community-scale effects of OA by imposing scenarios on a food web model of Puget Sound (Harvey et al., 2010, 2012). Specifically, variable levels of OA-driven changes in productivity were imposed on calcifying crustacean, mollusc and echinoderm groups and the food web-mediated impacts on the community as a whole were examined, via measures of ecosystem diversity and change in how energy moves through the food web. The impacts on groups that provide ecosystem services, such as fishery harvests, ecotourism opportunities, and forage for higher trophic levels, were also examined. Because of the high uncertainty inherent in this modelling exercise, results were evaluated through general comparisons of alternative scenarios and the ecological processes that underlie change in the food web, rather than as precise quantitative predictions.

Material and methods
Puget Sound food web model
The food web model for the central basin of Puget Sound (Harvey et al., 2010, 2012) was developed using the Ecopath with Ecosim (EwE) software version 5.1 (Christensen and Walters, 2004). In EwE, species or aggregated functional groups are treated as biomass pools regulated by gains (consumption, production, immigration) and losses (predation, fisheries, emigration). Biomass pools are directly linked to one another through trophic relationships or, if specified, life history relationships (e.g. juvenile and adult pools for a species), such that a change in one pool will affect the mass balance of other pools, depending on the strengths of the direct and indirect links between different pools. The discrete-time and differential equations that govern these processes are detailed elsewhere (Christensen and Walters, 2004).

The Puget Sound model features 65 functional groups, listed in Table 1, along with 15 fisheries distinguished by gear types. Harvey et al. (2010, 2012) describe in detail how the baseline model parameters were derived from the biological and ecological characteristics of each group. The food web spans nearly five trophic levels and features benthic, pelagic, and ubiquitous functional groups, including detrital pools, primary producers, invertebrates, fishes, marine mammals, and seabirds (Figure 1). Because less is known about the ecology of the highly diverse lower and middle trophic levels, many such species are coarsely aggregated into groups that represent 10s or 100s of species (Harvey et al., 2010, their Appendix A). The model's ability to simulate system dynamics, including the strength of top-down and bottom-up predator–prey control and the relative importance of phytoplankton

Table 1. Functional groups in the Puget Sound central basin food web model.

| Category, Functional groups	Category, Functional groups
Pinnipeds	**Benthic invertebrates (continued)**
Harbor seals	*Sea stars (E)*
Sea lions	*Sea urchins (E)*
	Other grazers (M)
Seabirds	*Small benthic crustaceans (C)*
Gulls	*Large sea cucumbers (E)*
Resident diving birds	*Predatory gastropods (M)*
Migratory diving birds	*Mussels (M)*
Nearshore diving birds	*Barnacles (C)*
Herbivorous birds	*Geoducks (M)*
Eagles	*Infaunal bivalves (M)*
	Soft infauna
Pelagic fishes	*Deposit feeders (E)*
Wild salmon (juveniles, adults)	Suspension feeders
Hatchery salmon (juveniles, adults)	Tunicates
Pink salmon (juveniles, adults)	
Pacific herring (juveniles, adults)	**Pelagic invertebrates**
Forage fish	*Microzooplankton (C)*
Surf perches	*Copepods (C)*
Pacific hake	*Euphausiids (C)*
	Small gelatinous zooplankton
Demersal fishes	Jellyfish
Spiny dogfish	*Macrozooplankton (C)*
Skates	Squid
Ratfish	
Pacific cod	**Primary producers**
Walleye pollock	Phytoplankton
Lingcod (juveniles, adults)	Benthic microalgae
Rockfish (juveniles, adults)	Benthic macroalgae
Piscivorous flatfish	Overstory kelp
Small-mouthed flatfish	Eelgrass
Small demersal fish	
	Microbial and detrital pools
Benthic invertebrates	Plant/algal material
Octopus	Salmon carcasses
Shrimp (C)	Detritus
Cancer crabs (age 0, age 1 +) (C)	Bacteria

Groups manipulated in the ocean acidification scenarios are in italics, and their category identified as follows: E = echinoderm, C = crustacea, M = mollusc. Spiny dogfish were excluded from the demersal fish group in analyses due to difficulty in assigning their primary habitat.

variability and fishing mortality, was assessed through a series of tuning exercises that fit model outputs to time-series data from the 1980s−2000 (Harvey et al., 2012).

Modelling response to OA
Selection of affected species
Research to date indicates that calcifying species will be most impacted by OA (Kroeker et al., 2010), so impacts of OA were imposed on all heterotrophic functional groups dominated by calcifiers (Table 1, Figure 1). These calcifying functional groups include many of the largest biomass pools in the model and are at low and intermediate trophic levels. Thus, they play important roles in transferring energy from primary producers to the rest of the food web. Although some non-calcifying organisms will likely be affected by OA (e.g. Palacios and Zimmerman, 2007; Beardall et al., 2009; Munday et al., 2012), patterns of response to OA in non-calcifying
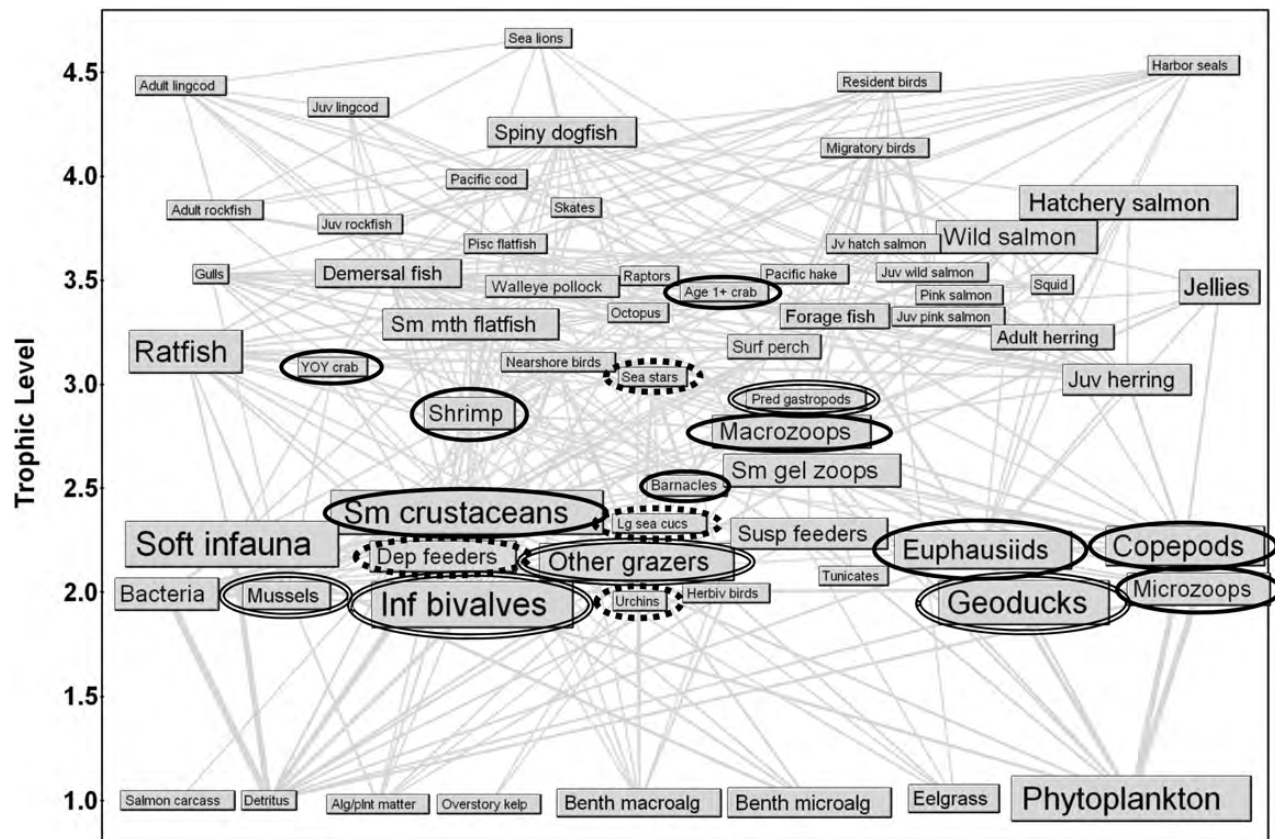
Figure 1. Food web model of Puget Sound's central basin, with 65 functional groups (Harvey *et al.*, 2010). Box size is proportional to biomass, and the width of connecting lines is proportional to energy flow from prey to predator. Functional groups included in ocean acidification scenarios are circled. Single line = crustaceans, double line = molluscs, dashed line = echinoderms.

organisms are highly uncertain, thus functional groups dominated by non-calcifiers were not directly manipulated.

Manipulating the EwE model

Within the dynamic Ecosim module of EwE, changes in biomass of consumer functional groups in the model occur according to the equation:

$$\frac{dB_i}{dt} = cg_i \sum_{j=1}^{n} f(B_j, B_i) - \sum_{j=1}^{n} f(B_i, B_j) + I_i - B_i(M_i + F_i + E_i) \tag{1}$$

where B is biomass, $f(B_j, B_i)$ a functional relationship used to predict consumption rates of all prey j by group i, $f(B_i, B_j)$ a functional relationship used to predict consumption rates of group i by all predators j, I immigration rate out of the ecosystem, M natural mortality, F fishing mortality, E emigration, g growth efficiency, and n number of functional groups. We used the scalar c to introduce forcing functions that simulate the long-term press perturbation of OA on susceptible functional groups' production rates (Table 1). In EwE, this is done by reducing the search rate for prey, effectively making the given functional group an inferior predator that consumes less prey per unit energy spent searching (Ainsworth *et al.*, 2011). This approach does not imply that foraging is the mechanism by which OA affects the species; we simply assume that, in an acidified ocean, vulnerable groups will have decreased productivity (defined as the

first part of Equation 1). We nested OA scenarios to allow for exploration of the food web-scale effects of OA mediated by vulnerability of individual functional groups or collections of functional groups. We developed scenarios in which:

(i) only one calcifying functional group was affected;

(ii) all calcifying crustacean, molluscan, or echinoderm functional groups were affected simultaneously (categorical scenarios);

(iii) all heterotrophic calcifying functional groups in the model were affected simultaneously (combined scenarios).

Given uncertainty both in the spatial and temporal development of OA in Puget Sound and how to model the response of functional groups to OA, forcing functions on the scalar c were linear decreases that, by the end of the 50-year scenario, imposed a 5% decrease in productivity for small strength scenarios, 15% decrease for moderate strength scenarios, and 25% decrease for substantial strength scenarios (i.e. $c = 0.95$, 0.85, or 0.75, respectively). Although we make a simplifying assumption of linearity, species' responses to OA likely will not track changes in pH in a one-to-one manner and future pH decreases are expected to be non-linear. Species are likely to have different tolerances to declines in pH and different breakpoints for non-linearity in their responses. Even if an individual species demonstrated a linear decline, the model operates on functional groups that often consist of multiple species; differences in the rates of change for individual species within an aggregate

functional group may result in a non-linear response of the group as a whole. Furthermore, while we recognize that pH changes in Puget Sound's main basin will vary with location and depth (Doney *et al.*, 2007; Feely *et al.*, 2010; Salathé *et al.*, 2010), the Puget Sound food web model's lack of spatial structure (Harvey *et al.*, 2010) necessitated simplifying assumptions. Results focus on the biomass of functional groups at the end of the 50-year model runs, not on how the food web changes over the course of the model runs.

Estimated changes to ecosystem services

At the end of each model run, two types of ecosystem services were calculated: fisheries yield from the food web and the biomass of functional groups that provide non-extractive ecosystem services (e.g. ecotourism, forage for higher trophic levels). To assess the magnitude of response to each scenario, results were compared with values from a baseline model run that did not include effects of OA. The discussion focuses on groups whose harvest or biomass changed by $\geq 10\%$ from the baseline model run, as smaller changes imply relatively weak food web effects that would be difficult to detect empirically above the noise of natural variation or sampling error.

EwE estimates fishery harvests by imposing user-defined fishing mortality rates, which were based on empirical landings data from the 1990s–2000s (Harvey *et al.*, 2010, their Appendix C). Instantaneous annual fishing mortality rates (the ratio of landings to total biomass) were fixed at the initial values for all harvested species throughout the 50-year model runs. Target biomass pools were lumped into 11 harvest groups, and annual landings (t km^{-2} year^{-1}) for each harvest group were summed for each model run.

Assessing changes to food web

Changes in the flow of energy through the food web caused by the OA scenarios were explored by evaluating changes in biomass, relative to the baseline model run, of pelagic and demersal fishes and the major lower to mid-trophic level functional groups not manipulated by the OA scenarios (soft infauna, suspension feeders, and small gelatinous zooplankton). Changes to diversity in the model food web were evaluated using Kempton's species diversity index (Q; Kempton and Taylor, 1976), as modified by Ainsworth and Pitcher (2006) for use with Ecosim output. This index calculates the evenness and richness of the food web by assessing the distribution of biomass among functional groups and changes in functional group biomass over time. For this study, a Q_{90} index was used:

$$Q_{90} = \frac{0.8S}{\log\left(\frac{R_2}{R_1}\right)} \quad (2)$$

where S represents the number of functional groups in the model and R_1 and R_2 represent the biomass values of the 10th and 90th percentile functional groups based on a cumulative biomass distribution with logarithmic bins (Ainsworth and Pitcher, 2006). Higher Q_{90} scores equate to higher levels of biodiversity. We report the percent change in diversity score between the baseline model run and various scenarios.

Results

The OA scenarios had different effects on biomass of the functional groups directly affected by them, some positive and some negative (Figure 2). Trophic interactions yielded biomass increases in some functional groups; for example, microzooplankton biomass

increased in response to the combined scenario due to the decline of their main predator, copepods. Crustacean functional groups were the most sensitive to the scenarios; in response to the
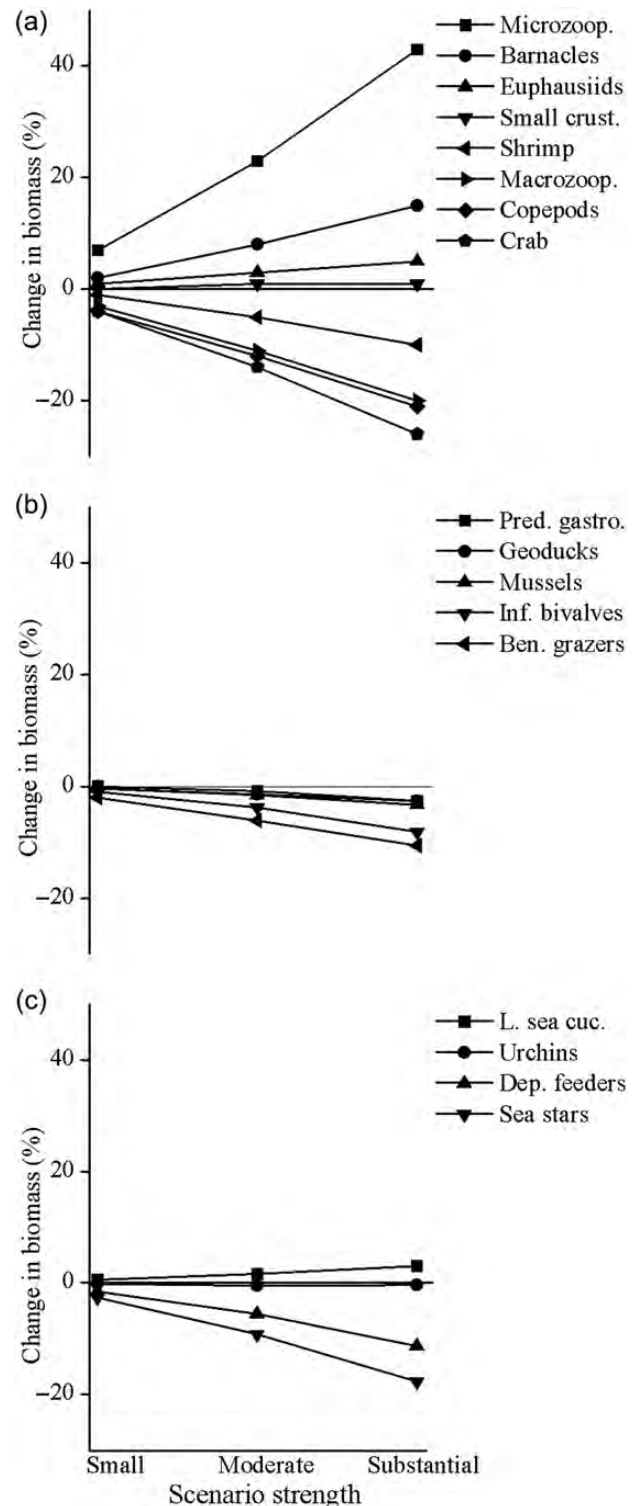
Figure 2. Percent change in biomass, relative to the baseline model run, of (**a**) crustaceans, (**b**) calcifying molluscs, and (**c**) echinoderms in response to the combined scenario at three different strengths (small, moderate, substantial).

substantial combined scenario, biomass change was greater than 10% for all crustacean functional groups except for euphausiids and small crustaceans. In comparison, sea stars, deposit feeders, and benthic grazers were the only mollusc and echinoderm functional groups to experience a change in biomass greater than 10%. Biomass of directly affected functional groups changed linearly with scenario strength (Figure 2); this result held for indirectly affected functional groups, but, for brevity, we do not show these results.

Fisheries yield

Most of the change in fisheries yield in response to the scenarios was due to their direct effects, rather than indirect trophic effects extending to finfish and cephalopods (Figure 3). The direction of change in fisheries yield was consistent across scenario strengths, and the magnitude of change increased linearly as productivity forcings increased (Figure S1).

The crustacea scenario caused fisheries yield of herring, shrimp, and *Cancer* crabs to decrease (Figure 3a). Changes in shrimp and *Cancer* crab yield were due to direct effects imposed by the OA

scenarios. The decrease in herring harvest was primarily caused by forced declines in copepods, their main prey. However, the negative impact of the copepod scenario on herring harvest was mediated, in part, by the macrozooplankton and euphausiid scenarios (Figure 4a). Macrozooplankton and euphausiids depress copepod abundance through predation and resource competition; therefore, reducing macrozooplankton and euphausiid biomass released some pressure on copepods and, in turn, benefitted herring. This chain of cascading events exemplifies the contradictory nature of many of the crustacean single-functional groups scenarios on the food web (Pace *et al.*, 1999). These contradictory effects cancelled each other out in the crustacea scenario (Figure 3a). For example, the positive effect of the copepod scenario on flatfish harvest was counteracted by the negative effect of the macrozooplankton scenario, and the highly negative effect of the euphausiid scenario on squid/octopus harvest was counteracted by the positive effect of the macrozooplankton scenario.

Bivalve harvest decreased by 8% in response to the substantial-strength mollusc scenario, even though a 25% decline in productivity was directly imposed on bivalves (Figure 3b). Various ecological
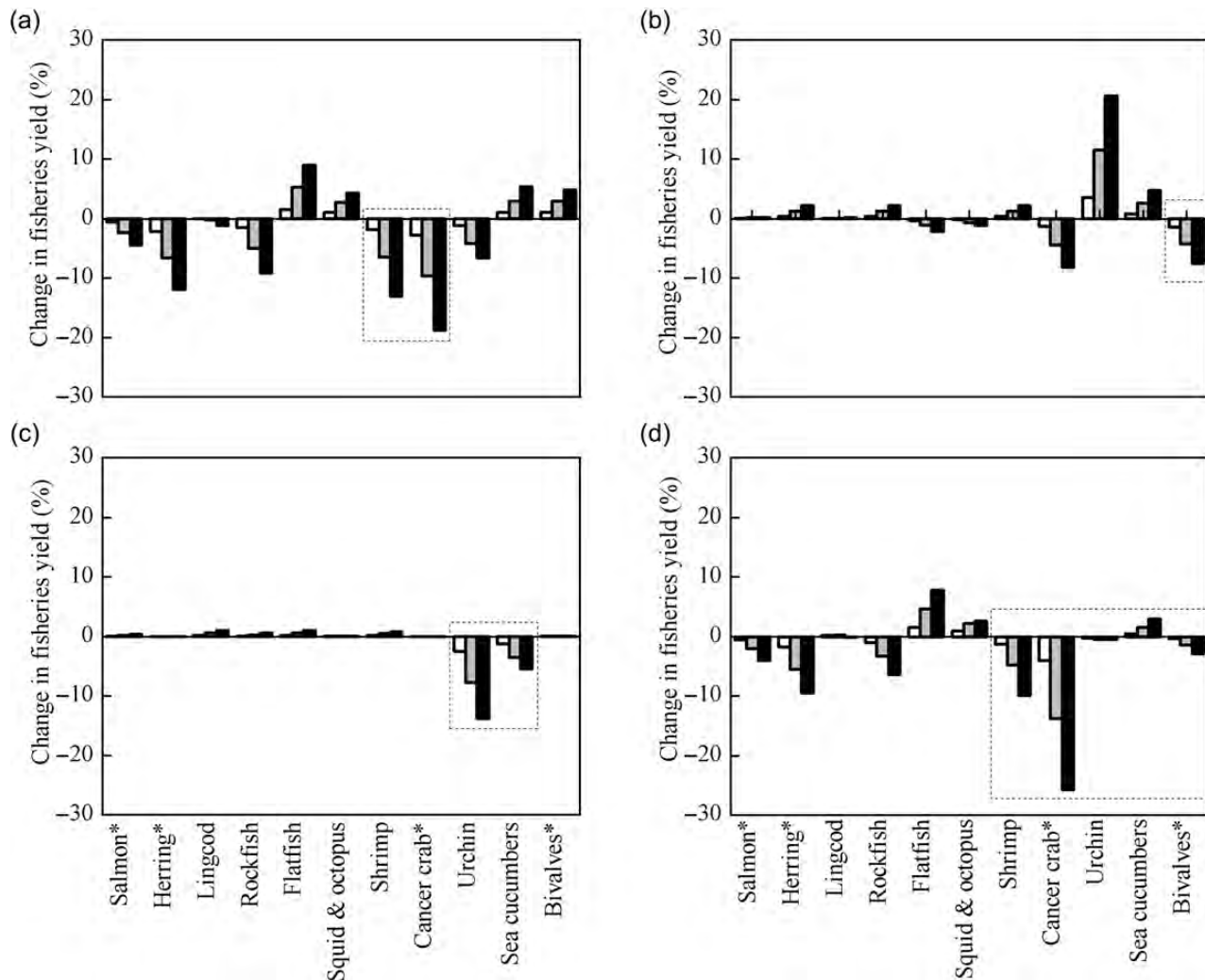
Figure 3. Percent change in fishery yields, relative to the baseline model run, in response to (**a**) crustacea, (**b**) calcifying mollusc, (**c**) echinoderm, and (**d**) combined scenarios of three strengths: small (white bars), moderate (grey bars), and substantial (black bars). Asterisk indicates central Puget Sound's largest fisheries by weight. Groups directly affected by the scenarios are enclosed by dashed boxes.
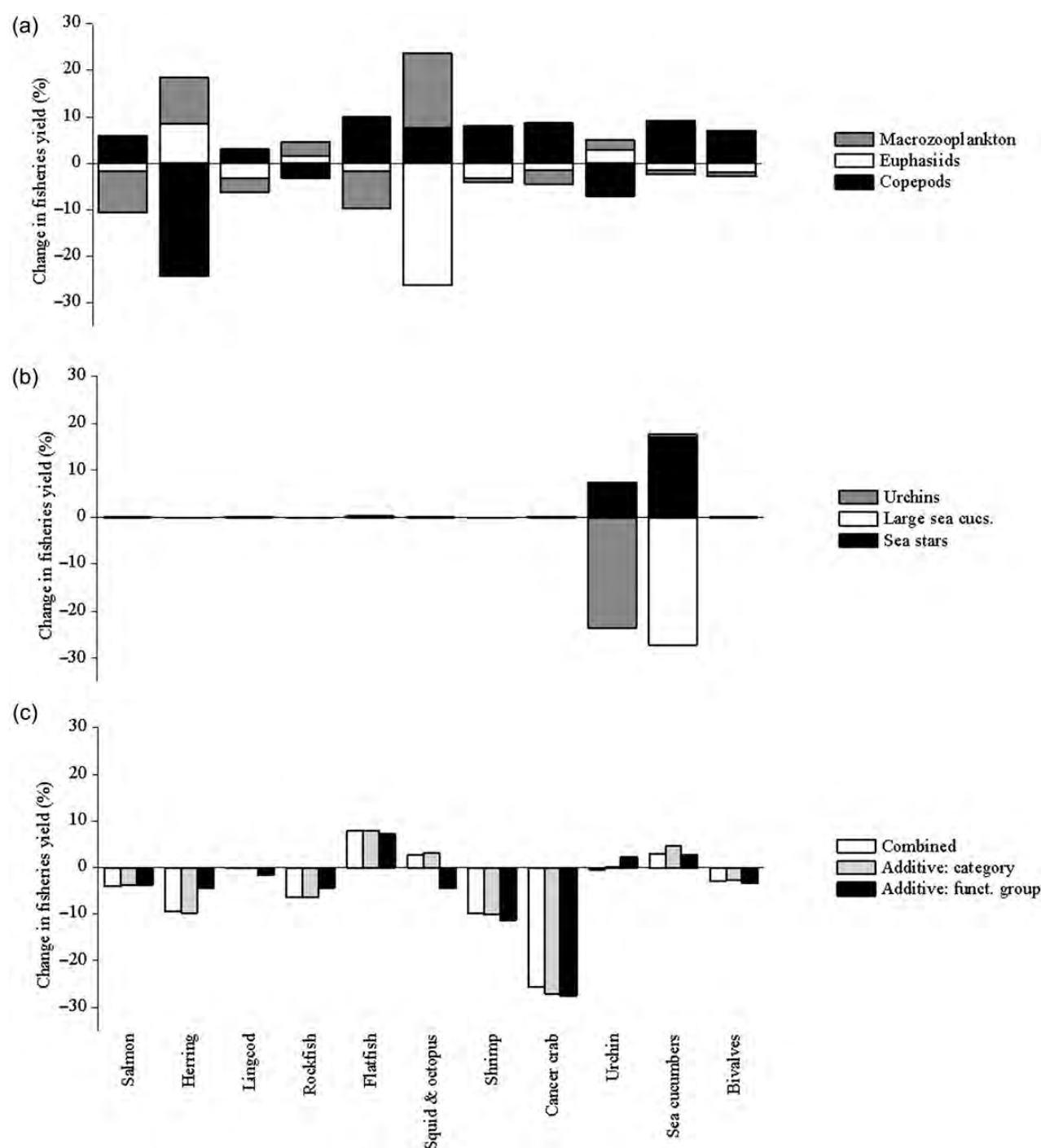
Figure 4. Percent changes in fishery yields, relative to the baseline model run, in response to (**a**) three single-functional group scenarios on crustaceans (macrozooplankton, euphausiids, or copepods) and (**b**) three single-functional group scenarios on echinoderms (urchins, large sea cucumbers, or seastars). Panel (**c**) presents changes in yield from the combined scenario (Combined), the sum of changes in yield from all categorical scenarios (Additive: category), and the sum of changes in yield from all single-functional groups scenarios (Additive: funct. group). All results are from substantial strength scenarios.

interactions shaped the change in biomass of the three functional groups that comprise the bivalve harvest: biomass of infaunal bivalves (small to medium-sized clams) decreased by 24% with forced declines in productivity countered by release from intra-functional group competition and an increase in phytoplankton food; mussel biomass decreased by 14% with forced declines in productivity countered by declines in predator populations (near-shore diving birds, surf perch) and a decrease in competition from infaunal bivalves; and geoduck (*Panopea generosa*) biomass decreased by just 6% because the species' long life cycle (maturity at 10+ years, longevity 100+ years) masked a slow population decline. Scenarios on benthic grazers, predatory gastropods, and

all calcifying molluscs increased urchin harvest because benthic grazers and predatory gastropods are, respectively, urchin competitors and predators. Reductions in echinoderm productivity had little impact on fisheries yield of groups other than echinoderms (Figure 3c). The sea star scenario increased both urchin and large sea cucumber yield due to reduced predation by predatory sea stars on both groups and release of large sea cucumbers from food competition with deposit-feeding sea stars (Figure 4b).

The biggest effect of the combined scenario was a decrease in *Cancer* crab yield; this effect was caused by both direct OA effects and the indirect effects of the mollusc scenario (Figure 3d). Urchin yield was unaffected by the combined scenario because the direct and indirect effects on yield cancelled each other. Other harvested groups (e.g. bivalves, sea cucumbers) experienced a similar cancelling-out of effects under the combined scenario, but to a lesser degree than urchins.

Generally, the impacts of single-functional-group and category-specific scenarios built additively on fisheries yield: the sum of all changes caused by either the single-functional-group scenarios or the categorical scenarios was almost equivalent to the changes caused by the combined scenario (Figure 4c). However, the additive nature of OA effects on fisheries yield was violated for herring, rockfish, urchins, and squid/octopus when the effects of the single-functional-group scenarios were compared to the combined scenarios and the crustacea scenario (not shown). This result indicates that the nature of how trophic interactions affect fisheries yield can be impacted by the identity of which crustacean functional groups are directly affected by OA.

Biomass of non-harvested vertebrates that provide ecosystem services

The copepod, euphausiid, and infaunal bivalve scenarios were the only single-functional-group scenarios to impact biomass of non-harvested vertebrates that provide ecosystem services (Figure 5a). The copepod scenario decreased biomass of forage fish, migratory diving birds, and gulls and increased biomass of nearshore diving birds. Copepods are a major prey source of forage fish, and migratory diving birds and gulls prey on forage fish. Nearshore diving bird biomass was sensitive to the copepod scenario because it increased biomass of two of their prey groups (infaunal bivalves and mussels). The euphausiid scenario had opposite, though smaller effects on the biomass of groups that provide ecosystem services; euphausiids compete with forage fish and have less trophic impact on the groups that copepod biomass influences. The crustacea scenario affected only forage fish and nearshore diving birds: the effects of the copepod scenario on migratory diving birds and gulls were cancelled by the effects of the euphausiid scenario (Figure 5b). The infaunal bivalve scenario caused a reduction in nearshore diving bird biomass, their predator. This result held for the mollusc scenario. The echinoderm scenarios had no effect on functional groups that provide non-extractive ecosystem services. The combined scenario caused a decrease in forage fish biomass; impacts of the categorical scenarios on all other groups cancelled each other due to their additive effects.

Flow of energy and food web diversity

Declines in crustacean and mollusc productivity (especially of copepods, small crustaceans, and benthic grazers) altered the structure of the food web, redirecting energy flow through several non-crustacean consumers (Figure 6). Small crustaceans eat soft infauna (e.g. polychaetes), compete with them for detritus, and
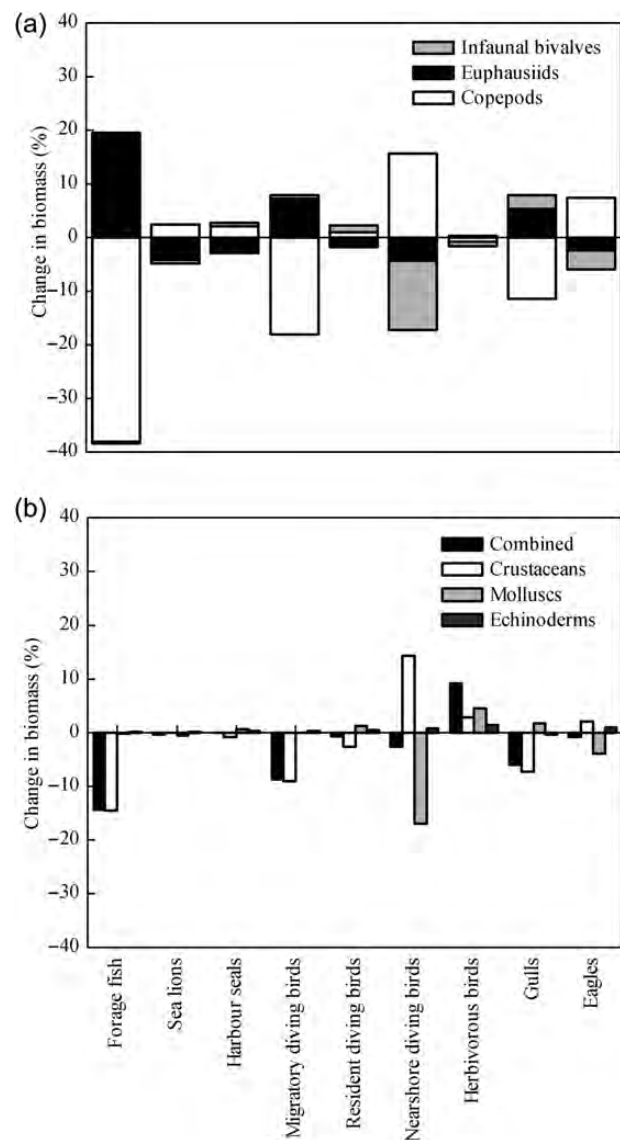
Figure 5. Percent change in forage fish, bird, and marine mammal biomass, relative to the baseline model run, in response to (**a**) three single-functional-group scenarios (infaunal bivlaves, euphausiids, copepods), and (**b**) categorical and combined scenarios. All results are from substantial strength scenarios.

support predator populations that also prey on soft infauna (e.g. small-mouthed flatfish). Small crustaceans also predate on suspension feeders and compete with them for detritus. Copepods are a competitor with suspension feeders and small gelatinous zooplankton for phytoplankton prey and with soft infauna for phytoplankton-derived detritus. Due to the importance of copepods in so many consumer diets, the copepod scenarios likely caused additional indirect, food web-mediated effects on soft infauna, suspension feeders and small gelatinous zooplankton. Benthic grazers predate on suspension feeders, compete with them for detritus, and support populations of predators (e.g. octopus) that predate on species that compete with suspension feeders for food (e.g. crab). The echinoderm scenarios had little influence on energy flow in the food web. The changes in energy flow through the food web caused by the OA scenarios had little effect on
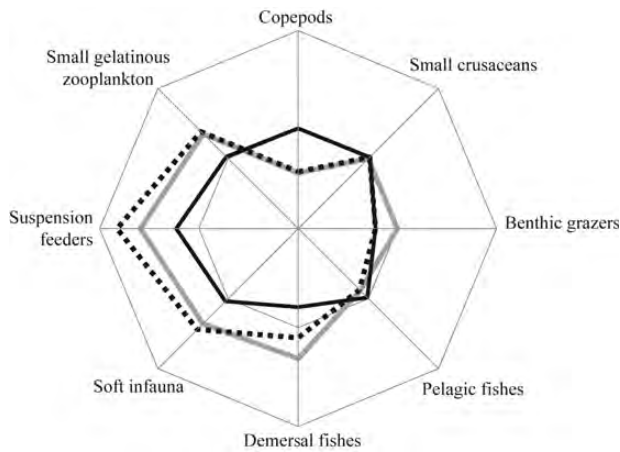
Figure 6. Proportional change in biomass, relative to the baseline model run, of pelagic and demersal fishes and selected lower- to mid-level trophic groups in response to the mollusc scenario (black line), crustacea scenario (grey line), and combined scenario (dotted line). Functional groups that comprise pelagic and demersal fishes groups are detailed in Table 1. The axial scale is linear, with the origin at 50% decrease in biomass, midline at no change in biomass, and edge at 50% increase in biomass. All results are from substantial strength scenarios.

pelagic fish biomass and mixed effects on demeral fish biomass (crustacea and combined scenarios increased demersal fish biomass, mollusc scenario decreased demersal fish biomass).

In general, the OA scenarios had a small impact on ecosystem diversity, as measured by Kempton's *Q*. The crustacea and combined scenarios caused identical increases in diversity at all scenario strengths (small = 2%, moderate = 3%, substantial = 5%). The copepod scenarios drove this increase (small = 2%, moderate = 7%, substantial = 9%), but were countered somewhat by decreases in diversity in response to the euphausiid scenarios (moderate = −2%, substantial = −1%). The substantial mollusc scenario caused a small increase in diversity (2%), due mostly to the infaunal bivalve scenario. The echinoderm scenario did not affect diversity scores (0% change), due to the positive impacts of the sea star scenario (moderate and substantial = 2%) balancing with the negative impacts of the large sea cucumber scenario (moderate = −1%, substantial = −2%).

Discussion

This study highlights how OA-induced changes in a few key groups, such as copepods, can have large ecological consequences due to complex food web interactions. The OA scenarios affected ecosystem services in ways that were generally additive (comparing single-functional-group scenarios to categorical scenarios, and categorical scenarios to the combined scenario), sometimes yielding a net result of no change. These results emphasize the importance of considering the impacts of OA in the context of the entire food web and of correctly characterizing which groups are susceptible to OA. The impact of OA on a community cannot necessarily be predicted by a community's or group of species' average direct responses to OA, especially because, in some systems, the groups that seem most susceptible to OA (molluscs and echinoderms) may influence the food web less than the groups that are less susceptible to OA (Hall-Spencer *et al.*, 2008; Wootton *et al.*, 2008; Hale *et al.*, 2011; Kroeker *et al.*, 2011).

This study's findings indicate that the direct impacts of OA can be masked or dampened by trophic effects. For example, the direct effects of the urchin scenario on the functional group's biomass were entirely offset by decreased productivity of two predators (sea stars, predatory gastropods) and a competitor (benthic grazers). Furthermore, the indirect effects of OA can also have contradictory impacts on members of the food web: many of the indirect effects of the copepod scenarios (e.g. decreased biomass of migratory diving birds and herring) were countered by those of other crustacea single-functional-group scenarios, like the macrozooplankton and euphausiid scenarios. That trophic interactions dampened the impacts of OA on the food web suggests, counter-intuitively, that having a large number of species affected by OA can lead to less ecosystem change than having only a few species affected by OA. This hypothesis, which is specific to the Puget Sound food web, should be tested by other models and field observations. Field and mesocosm studies from other locales suggest that trophic interactions, such as competition and predation, influence community response to OA, but none yet have documented dampening (Wootton *et al.*, 2008; Hale *et al.*, 2011; Kroeker *et al.*, 2011).

Ecosystem change

Although the OA scenarios caused little change in food web diversity, they changed the flow of energy through the food web. This change favoured the flow of energy through soft infauna, suspension feeders, and small gelatinous zooplankton, instead of through calcifiers, which affected demersal, but not pelagic, fish biomass. Small benthic crustaceans, infaunal bivalves, and soft infauna are among the most important groups in this model food web, in terms of both biomass and the diets of higher trophic levels (Harvey *et al.*, 2012). While some fishes (e.g. small-mouthed flatfishes, ratfish *Hydrolagus colliei*) feed opportunistically on all three groups, many other demersal fishes feed more heavily on benthic crustaceans. A shift toward a benthic prey base dominated by polychaetes may thus lower carrying capacities for some demersal consumers. Communities exposed to high CO_2 environments (i.e. volcanic vent sites) can display significant shifts in the patterns of species abundance compared to neighbouring, uninfluenced communities due to differences in species sensitivity to CO_2 and changes in competitive interactions among species (Hall-Spencer *et al.*, 2008; Kroeker *et al.*, 2013), suggesting that OA alone may be enough to cause large ecological change. Diversity scores increased in response to the combined and crustacea scenarios because of the more even balance in biomass among calcifying and non-calcifying functional groups at lower and mid-trophic levels and among pelagic and demersal fish functional groups. The way that we assessed diversity does not account for potential local extirpations of OA-sensitive species.

Understanding the impacts of ocean acidification

The results of this modelling exercise should be considered more from a conceptual level than as a quantitative prediction about what will happen to the Puget Sound food web under OA. Conceptually, the results indicate that (i) the effects of OA transfer to species not directly vulnerable to increases in CO_2; (ii) food web interactions can dampen ecosystem effects of OA as predators, prey, and competitors for a given species might all be impacted simultaneously; and (iii) the ecosystem response is dependent upon which particular species group is most sensitive to OA. However, in interpreting specific results for Puget Sound it should be

recognized that the OA scenarios were limited by knowledge of how OA will impact marine species (Kroeker *et al.*, 2010). Even in some well-studied taxa, generalizing population response to OA is difficult (Miller *et al.*, 2009; Hale *et al.*, 2011; Russell *et al.*, 2011), which makes predicting the shape and magnitude of response of species aggregates (e.g. functional groups) extremely challenging.

Our scenarios develop an unlikely situation in which all calcifiers—predators, prey, and competitors—respond to OA with identical declines in productivity. The linear scaling of results with scenario strength suggests that scenario strength plays a role in controlling the size of the effects we observed, but does not influence their nature. While the scenarios we imposed on the Puget Sound model may be more or less severe than what is likely to occur over the next 50 years, they yield signals about the potential direction and nature of community change. Differential sensitivity to OA among functional groups could yield patterns in food web response other than those we observed here; those effect size and response patterns could be elucidated through careful synthesis of ongoing and future field, experimental, and modelling research. The generic scenarios we employed do not capture many types of acute species responses, such as recruitment failure or extirpation, and could not adequately capture other types of changes, such as alteration of the nutritional content of primary producers (Iglesias-Rodriguez *et al.*, 2008), shifts in predator–prey interactions (Bibby *et al.*, 2007; Ferrari *et al.*, 2011), and changes in abundance of habitat-forming species like eelgrass (Palacios and Zimmerman, 2007; Pandolfi *et al.*, 2011). Considering the cumulative effects of other aspects of climate change (Harley *et al.*, 2006; Ainsworth *et al.*, 2011; Doney *et al.*, 2012) and how they will interact with other human-caused stressors (Doney *et al.*, 2007; Pascal *et al.*, 2010; Griffith *et al.*, 2011) is beyond the scope of this exercise, but important to consider. Ecological communities subjected to numerous disturbances, including ones that are low-intensity and chronic, or high-intensity and rare, can change significantly, sometimes into new states (Paine *et al.*, 1998).

Ecosystem models are useful platforms for exploring potential community-level effects of OA through a variety of mechanisms and pathways. As with prior ecosystem modelling studies (Kaplan *et al.*, 2010; Griffith *et al.*, 2011, 2012), we forced the impacts of OA via a bottom-up process: reduced productivity or direct natural mortality on calcifiers. Alternative scenarios might be driven by top-down effects, in which impacted species are more vulnerable (*sensu* Christensen and Walters, 2004) to predators through mechanisms such as reduced avoidance behaviour, weaker calcareous shells, or slowed growth that prevents them from exceeding predator gape limits; all of these mechanisms can be included in contemporary ecosystem models. Innovative field and lab studies will be required to quantify the actual mortality rates caused by top-down and bottom-up drivers so that these mechanisms can be modelled effectively (Kaplan *et al.*, 2010). Ecosystem models also offer insight into the sensitivity of a whole system to OA effects on a subset of its components. For example, in both our study and that of Kaplan *et al.* (2010), OA effects directed at pelagic calcifiers resulted in strong system-wide responses. In contrast, Griffith *et al.* (2011, 2012) only considered direct OA impacts on benthic invertebrates. Ongoing food web modelling studies should consider both pelagic and benthic calcifiers, particularly the strong interactors, where evidence indicates sensitivity to OA effects; the extent of OA impacts may relate to the degree of benthic-pelagic coupling in the ecosystem. The Atlantis marine ecosystem modelling framework used by Kaplan *et al.* (2010) and

Griffith *et al.* (2011, 2012) is spatially explicit and coupled to physical circulation models; this framework should allow for greater spatial resolution of expected OA effects on marine communities as pH, pCO$_2$, and related variables are included as model currencies.

As different ecological mechanisms are considered in the future, other external drivers might be introduced, such as fishing and ocean warming, to see if OA effects are mitigated or exacerbated in a cumulative impacts scenario (e.g. Kaplan *et al.*, 2010; Ainsworth *et al.*, 2011; Griffith *et al.*, 2012). Our experience with the central basin Puget Sound EwE model suggests that current levels of fishing in the system are low and have little effect on ecosystem function (Harvey *et al.*, 2012), but ecosystem modelling studies of Australian marine systems predict synergistic effects of fishing and OA under some management regimes (Griffith *et al.*, 2011, 2012). Thus, studying the interactive and cumulative impacts of OA with fishing and other environmental changes is necessary in order to set responsible management and conservation goals in systems impacted by OA (Kaplan *et al.*, 2010).

The results of this study were determined by the EwE modelling framework. For example, migratory species, such as salmon and sea lions, are present in the Puget Sound model for only a portion of their life cycle. The responses of these higher-trophic-level functional groups to the OA scenarios might be modelling artefacts, as we could not simulate the impacts of OA on their open-ocean prey and were not able to incorporate potential OA-induced shifts in migratory behaviour. The EwE model also does not allow switching to novel prey, which may occur with changing ocean conditions (Le Quesne and Pinnegar, 2012), nor does it include other potential ecological responses to change (e.g. species invasion). How potential increases in populations of habitat-producing species affect the populations of other functional groups was also not addressed in this modelling exercise. For example, eelgrass may be "fertilized" by OA, altering the food web, in part by creating more habitat for other species (Plummer *et al.*, 2013). Finally, the indirect effects presented here are entirely dependent upon our assumptions about the structure and functioning of the food web; although the model was iteratively tuned to ~20 years of contemporary time-series data, that process was constrained by different sources of uncertainty (Harvey *et al.*, 2012). Given these caveats, the outputs presented here are best viewed as hypotheses of potential impacts; such is the case with most complex ecosystem models (Link *et al.*, 2012). Model results require validation through careful monitoring of directly and indirectly affected groups, experiments that elucidate the variety of ways that OA could impact species biology, and comparisons with predictions from other, independent modelling platforms, such as Atlantis (Kaplan *et al.*, 2010; Griffith *et al.*, 2011).

Modelling exercises such as this one provide information that could help managers incorporate OA into resource planning. For example, ocean-acidification-induced changes in marine resources are important to consider when designing fisheries management schemes and monitoring activities (e.g. individual fishing quotas; Kaplan *et al.*, 2010). However, practical application requires more precision than is available in this first generation exercise. Increased information on the response of individual species to OA, local-scale projections of ocean carbon chemistry, and modelling tools that allow more nuanced modelling of direct and indirect effects of OA are needed to better estimate the structure of future ocean ecosystems.

Supplementary data

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References

Ainsworth, C. H., and Pitcher, T. J. 2006. Modifying Kempton's species diversity index for use with ecosystem simulation models. Ecological Indicators, 6: 623–630.

Ainsworth, C. H., Samhouri, J. F., Busch, D. S., Chueng, W. W. L., Dunne, J., and Okey, T. A. 2011. Potential impacts of climate change on Northeast Pacific marine fisheries and food webs. ICES Journal of Marine Science, 68: 1217–1229.

Beardall, J., Stojkovic, S., and Larsen, S. 2009. Living in a high CO_2 world: impacts of global climate change on marine phytoplankton. Plant Ecology & Diversity, 2: 191–205.

Bibby, R., Cleall-Harding, P., Rundle, S., Widdicombe, S., and Spicer, J. I. 2007. Ocean acidification disrupts induced defenses in the intertidal gastropod *Littorina littorea*. Biology Letters, 3: 669–701.

Caldeira, K., and Wickett, M. E. 2003. Anthropogenic carbon and ocean pH. Nature, 425: 365.

Christensen, V., and Walters, C. J. 2004. Ecopath with Ecosim: methods, capabilities and limitations. Ecosystem Modeling, 172: 109–139.

Cohen, A. L., and Holcomb, M. 2009. Why corals care about ocean acidification: uncovering the mechanism. Oceanography, 22: 118–127.

Doney, S. C., Mahowald, N., Lima, I., Feely, R. A., Mackenzie, F. T., Lamarque, J. F., and Rasch, P. J. 2007. Impact of anthropogenic atmospheric nitrogen and sulfur deposition on ocean acidification and the inorganic carbon system. Proceedings of the National Academy of Sciences of the United States of America, 104: 14580–14585.

Doney, S. C., Ruckelshaus, M. H., Duffy, J. E., Barry, J. P., Chan, F., English, C., Galindo, H. M., et al. 2012. Climate change impacts on marine ecosystems. Annual Review of Marine Science, 4: 11–37.

Fabricius, K. E., Langdon, C., Uthicke, S., Humphrey, C., Noonan, S., De'ath, G., Okazaki, R., et al. 2011. Losers and winners in coral reefs acclimatized to elevated carbon dioxide concentrations. Nature Climate Change, 1: 165–169.

Feely, R. A., Alin, S. R., Newton, J., Sabine, C. L., Warner, M., Devol, A., Krembs, C., et al. 2010. The combined effects of ocean acidification, mixing, and respiration on pH and carbonate saturation in an urbanized estuary. Estuarine, Coastal and Shelf Science, 88: 442–449.

Feely, R. A., Sabine, C. L., Hernandez-Ayon, J. M., Ianson, D., and Hales, B. 2008. Evidence for upwelling of corrosive "acidified" water onto the continental shelf. Science, 320: 1490–1492.

Feely, R. A., Sabine, C. L., Lee, K., Berelson, W., Kleypas, J., Fabry, V. J., and Millero, F. J. 2004. Impact of anthropogenic CO_2 on the $CaCO_3$ system in the oceans. Science, 305: 362–366.

Ferrari, M. C. O., McCormick, M. I., Munday, P. L., Meekan, M. G., Dixson, D. L., Lonnstedt, Ö., and Chivers, D. P. 2011. Putting prey and predator into the CO_2 equation – qualitative and quantitative effects of ocean acidification on predator–prey interactions. Ecology Letters, 14: 1143–1148.

Griffith, G. P., Fulton, E. A., Gorton, R., and Richardson, A. J. 2012. Predicting interactions among fishing, ocean warming, and ocean acidification in a marine system with whole-ecosystem models. Conservation Biology, 26: 1145–1152.

Griffith, G. P., Fulton, E. A., and Richardson, A. J. 2011. Effects of fishing and acidification-related benthic mortality on the southeast Australian marine ecosystem. Global Change Biology, 17: 3058–3074.

Hale, R., Calosi, P., McNeill, L., Mieszkowska, N., and Widdicombe, S. 2011. Predicted levels of future ocean acidification and temperature rise could alter community structure and biodiversity in marine benthic communities. Oikos, 120: 661–674.

Hall-Spencer, J. M., Rodolfo-Metalpa, R., Martin, S., Ransome, E., Fine, M., Turner, S. M., Rowley, S. J., et al. 2008. Volcanic carbon dioxide vents show ecosystem effects of ocean acidification. Nature, 454: 96–99.

Harley, C. D. G., Hughes, A. R., Hultgren, K. M., Miner, B. G., Sorte, C. J. B., Thornber, C. S., Rodriguez, L. F., et al. 2006. The impacts of climate change in coastal marine systems. Ecology Letters, 9: 228–241.

Harvey, C. J., Bartz, K. K., Davies, J., Francis, T. B., Good, T. P., Guerry, A. D., Hanson, B., et al. 2010. A mass-balance model for evaluating food web structure and community-scale indicators in the central basin of Puget Sound. U.S. Dept. Commerce, NOAA Technical Memorandum NMFS-NWFSC-106. 180 pp.

Harvey, C. J., Williams, G. D., and Levin, P. S. 2012. Food web structure and trophic control in central Puget Sound. Estuaries and Coasts, 35: 821–838.

Hauri, C., Gruber, N., Plattner, G-K., Alin, S., Feely, R. A., Hales, B., and Wheeler, P. A. 2009. Ocean acidification in the California current system. Oceanography, 22: 61–71.

Hautmann, M., Benton, M. J., and Tomašových, A. 2008. Catastrophic ocean acidification at the Triassic-Jurassic boundary. Neues Jahrbuch für Geologie und Paläontologie – Abhandlungen, 249: 119–127.

Hinga, K. R. 2002. Effects of pH on coastal marine phytoplankton. Marine Ecology Progress Series, 238: 281–300.

Hofmann, G. E., Smith, J. E., Johnson, K. S., Send, U., Levin, L. A., Micheli, F., Paytan, A., et al. 2011. High-frequency dynamics of ocean pH: a multi-ecosystem comparison. PLoS ONE, 6: pe28983.

Iglesias-Rodriguez, M. D., Halloran, P. R., Rickaby, R. E. M., Hall, I. R., Colmenero-Hidalgo, E., Gittins, J. R., Green, D. R. H., et al. 2008. Phytoplankton calcification in a high-CO_2 world. Science, 320: 336–340.

Kaplan, I. C., Levin, P. S., Burden, M., and Fulton, E. A. 2010. Fishing catch shares in the face of global change: a framework for integrating cumulative impacts and single species management. Canadian Journal of Fisheries Science, 67: 1968–1982.

Kempton, R. A., and Taylor, L. R. 1976. Models and statistics for species diversity. Nature, 262: 818–820.

Kroeker, K. J., Kordas, R. L., Crim, R. N., and Singh, G. G. 2010. Meta-analysis reveals negative yet variable effects of ocean acidification on marine organisms. Ecology Letters, 13: 1419–1434.

Kroeker, K. J., Micheli, F., and Gambi, M. C. 2013. Ocean acidification causes ecosystem shifts via altered competitive interactions. Nature Climate Change, 3: 156–159.

Kroeker, K. J., Micheli, F., Gambi, M. C., and Martz, T. R. 2011. Divergent ecosystem responses within a benthic marine community to ocean acidification. Proceedings of the National Academy of Sciences of the United States of America, 108: 14515–14520.

Kump, L. R., Bralower, T. J., and Ridgwell, A. 2009. Ocean acidification in deep time. Oceanography, 22: 94–107.

Le Quesne, W. J. F., and Pinnegar, J. K. 2012. The potential impacts of ocean acidification: scaling from physiology to fisheries. Fish and Fisheries, 13: 333–344.

Link, J. S., Ihde, T. F., Harvey, C. J., Gaichas, S. K., Field, J. C., Brodziak, J. K. T., Townsend, H. M., et al. 2012. Dealing with uncertainty in ecosystem models: the paradox of use for living marine resource management. Progress in Oceanography, 102: 102–114.

Miller, A. W., Reynolds, A. C., Sobrino, C., and Riedel, G. F. 2009. Shellfish face uncertain future in high CO_2 world: influence of

acidification on oyster larvae calcification and growth in estuaries. PLoS ONE, 4: pe5661.

Munday, P. L., McCormick, M. I., and Nilsson, G. E. 2012. Impact of global warming and rising CO_2 levels on coral reef fishes: what hope for the future? The Journal of Experimental Biology, 215: 3865–3873.

Pace, M. L., Cole, J. J., Carpenter, S. R., and Kitchell, J. F. 1999. Trophic cascades revealed in diverse ecosystems. Trends in Ecology & Evolution, 14: 483–488.

Paine, R. T., Tegner, M. J., and Johnson, E. A. 1998. Compounded perturbations yield ecological surprises. Ecosystems, 1: 535–545.

Palacios, S. L., and Zimmerman, R. C. 2007. Response of eelgrass *Zostera marina* to CO_2 enrichment: possible impacts of climate change and potential for remediation of coastal habitat. Marine Ecology Progress Series, 344: 1–13.

Pandolfi, J. M., Connolly, S. R., Marshall, D. J., and Cohen, A. L. 2011. Projecting coral reef futures under global warming and ocean acidification. Science, 333: 418–422.

Pascal, P.-Y., Fleeger, J. W., Galvez, F., and Carman, K. R. 2010. The toxicological interaction between ocean acidity and metals in coastal meiobenthic copepods. Marine Pollution Bulletin, 60: 2201–2208.

Pelejero, C., Calvo, E., and Hoegh-Guldberg, O. 2010. Paleoperspectives on ocean acidification. Trends in Ecology & Evolution, 25: 332–344.

Plummer, M. L., Harvey, C. J., Anderson, L., Guerry, A. D., and Ruckelshaus, M. H. 2013. The role of eelgrass in marine community interactions and ecosystem services: results from ecosystem-scale food web models. Ecosystems, 16: 237–251.

Russell, B. D., Harley, C. D. G., Wernberg, T., Mieszkowska, N., Widdicombe, S., Hall-Spencer, J. M., and Connell, S. D. 2011. Predicting ecosystem shifts requires new approaches that integrate the effects of climate change across entire systems. Biology Letters, doi: 10.1098/rsbl.2011.0779.

Salathé, E., Leung, L., Qian, Y., and Zhang, Y. 2010. Regional climate model projections for the State of Washington. Climatic Change, 102: 51–75.

Wootton, J. T., Pfister, C. A., and Forester, J. D. 2008. Dynamic patterns and ecological impacts of declining ocean pH in a high-resolution multi-year dataset. Proceedings of the National Academy of Sciences of the United States of America, 105: 18848–18853.

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